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Effects of Spatial Distribution and Reproductive Biology on *in situ* Fertilization Rates of a Broadcast-Spawning Invertebrate

RAFEL COMA[1] AND HOWARD R. LASKER[2]

Department of Biological Sciences, State University of New York at Buffalo, P.O. Box 601300, Buffalo, New York 14260-1300

Abstract. *In situ* fertilization was examined in the gorgonian *Pseudoplexaura porosa* during 1994 and 1995 spawning events in the San Blas Islands, Panama, to assess spatial and temporal variation in fertilization success and to determine whether *in situ* fertilization was sperm limited. Fertilization rates did not differ significantly between years (60% vs. 55%), but monthly means were significantly different, ranging from 22% to 66%. Fertilization rate varied among days, ranging from 0 to 85%; 80% of this variability was explained by daily variation in the number of colonies that spawned. A weighted average of *in situ* fertilization rates suggests that 67% or more of spawned eggs are fertilized in nature. Sperm limitation did not occur on the nights when most of the colonies synchronously spawned and when most of the eggs were released. Eggs collected downstream of the population often had higher fertilization rates than eggs collected either adjacent to their source colony or eggs collected in the middle of the population, which indicates that in dense populations, eggs may have multiple opportunities to be fertilized. Traits such as highly synchronous spawning, high fecundity, large egg size, large polyps, and large colonies directly and indirectly enhance *P. porosa* gamete production and fertilization. These life-history traits reduce the effects of gamete dilution during spawning events and thus decrease the importance of sperm limitation in the population dynamics of *P. porosa*.

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[1] Current address: Institut de Ciències del Mar-CSIC, Passeig Joan de Borbó s/n, 08039 Barcelona, Spain.

[2] Author to whom correspondence should be addressed.

Introduction

Whether or not fertilization rates constrain the reproductive success of free-spawning organisms has become a subject of increasing interest in the last 10 years (see Levitan, 1995, for review). Despite a growing number of studies on fertilization rates, the questions still remain whether low fertilization rates are common, whether low fertilization rates are caused by sperm limitation, whether fertilization rates limit reproductive success, and whether morphologies and behaviors that enhance fertilization act as constraints on the life-history evolution of broadcast-spawning taxa. We examined the fertilization rates of the Caribbean gorgonian *Pseudoplexaura porosa* in an effort to address these questions.

The conclusion that fertilization success is an important factor controlling the overall reproductive success of broadcast-spawning species comes from three types of data: observations of low fertilization rates during natural spawning events; experimental manipulations indicating that sperm density can limit fertilization success; and hydrodynamic models of gamete dilution. Low fertilization rates have been reported in taxa ranging from coelenterates to fishes (Petersen, 1991; Oliver and Babcock, 1992; Babcock and Mundy, 1992; Babcock *et al.*, 1992; Petersen *et al.*, 1992; Brazeau and Lasker, 1992; and Levitan, 1995). Moreover, fertilization rates are highly variable: even species with high average fertilization rates may exhibit cases of very low fertilization (*e.g.*, Sewell and Levitan, 1992), and conversely, species with low fertilization rates sometimes demonstrate high rates when observed over many days (*e.g., P. kuna;* Lasker *et al.*, 1996).

When they occur, low fertilization rates have generally

been attributed to sperm limitation. The only experimental demonstration of sperm limitation during natural spawning events is that of Lasker *et al.* (1996), who found that incubating naturally spawned eggs with supplemental sperm enhanced the fertilization rates of *Plexaura kuna*. Field experiments that report decreasing fertilization rates with distance downstream from spawning males again suggest that sperm density limits fertilization success (Pennington, 1985; Yund, 1990; Levitan, 1991; Levitan *et al.*, 1991, 1992; Babcock *et al.*, 1994; Brazeau and Lasker, 1992; Oliver and Babcock, 1992; Benzie *et al.*, 1994; Benzie and Dixon, 1994; Yund and McCartney, 1994; Levitan, 1995; Levitan and Young, 1995; Lasker *et al.*, 1996; Coma and Lasker, 1997). Although the effects of the downstream dilution of sperm can be lessened by synchronous spawning, among many species only a small proportion of the population participates in natural spawning events (Randall *et al.*, 1964; Mosher, 1982; Pennington, 1985; Michin, 1987; Levitan, 1988; Pearse *et al.*, 1988; McEuen, 1988; Babcock and Mundy, 1992; Babcock *et al.*, 1992; Gladstone, 1992; Beiring and Lasker, unpubl. data).

Hydrodynamic models and measurements of turbulent diffusion and the dilution of sperm also predict that fertilization rates should be low under many circumstances (Denny, 1988; Denny and Shibata, 1989; Lasker and Stewart, 1993; Levitan and Young, 1995; Lasker and Kapela, 1997). However, the predictions of those models are dependent on variables such as the rate of gamete release and net flow, and several authors have reported cases in which high fertilization rates are predicted (Denny *et al.*, 1992; Benzie *et al.*, 1994; and Levitan and Young, 1995).

Sperm limitation is not the only cause of low fertilization rates. For example, Levitan (1996a) reports differences in quality among sea urchin eggs, and similar effects have been observed among gorgonians (Lasker, unpubl. data). In addition, Mead and Denny (1995) have identified hydrodynamic conditions that interfere with sperm-egg interactions regardless of the concentration of sperm. Thus the commonness and causes of fertilization limitation are unclear and may be species specific.

Caribbean gorgonians are among the few taxa in which fertilization rates can be predictably and directly measured during natural spawning events. Many gorgonians exhibit synchronous spawning (Kinzie, 1970; Brazeau and Lasker, 1989, 1990), and the large eggs released by octocorals can be collected from the water column (Lasker *et al.*, 1996) or from the surface of the colony (Brazeau and Lasker, 1992). Although there are some overlaps between species in the timing of spawning, many taxa spawn on different days or at different times of day, allowing the collection of monospecific groups of gametes. The gorgonians studied to date have the lowest fertilization rates that have been measured *in situ* (*Briareum asbestinum* <0.01%–6%, Brazeau and Lasker, 1992; *Plexaura kuna* on average 26.4%, data from Lasker *et al.*, 1996). Lasker *et al.* (1996) also provided data on fertilization success in *Pseudoplexaura porosa*, noting that high fertilization rates (including some >80%) were more common in *P. porosa* than in *P. kuna*. These species appeared to differ in their fertilization rates and in the importance of sperm limitation. In this paper we expand our observations of *P. porosa* and show how reproductive strategy affects fertilization success in this species.

Material and Methods

Fieldwork was conducted at Korbiski reef, a patch reef located near the Smithsonian Tropical Research Institute (STRI) field station in the San Blas Islands, Panama. *Pseudoplexaura porosa* is a gonochoric broadcast spawner with a 1:1 sex ratio; it spawns in highly predictable events that occur shortly after sunset after the summer full moons (Lasker *et al.*, 1996; Ross and Lasker, unpubl. data). *P. porosa* is the second most abundant gorgonian on Korbiski reef (Lasker *et al.*, 1988) and, because of the size of its colonies (up to 250 cm in height), one of the dominant members of the benthos. The *P. porosa* population at Korbiski is most dense in a 150-m^2 area on the eastern side of the reef along a channel that separates Korbiski from an adjacent reef. The colonies at Korbiski were labeled and mapped. All colonies taller than 50 cm were measured, and a fragment was collected for sex identification.

Field collections were made during all spawning events in 1994 (June to September) and during June, July, and August in 1995. Eggs were collected from the water column shortly after they were released from colonies. Scuba divers positioned downstream of either specific colonies or the whole population collected the eggs (700 μm in diameter) in 60-ml plastic syringes. The syringes containing the collected eggs were brought to the STRI field station and after 0.5–1.5 hours all eggs were counted, placed in 120-ml polypropylene specimen cups, and incubated with seawater that had been collected prior to the start of spawning (sperm-free seawater). Containers were suspended from the field station dock to maintain temperature and provide some stirring. After 12 h the developing embryos were counted with the aid of a stereomicroscope. That value was used as the estimator of the number of eggs that had been fertilized. Results are expressed as percent fertilization and were arctan transformed prior to statistical analysis. Lasker *et al.* (1996) discussed the biases inherent to these procedures and concluded that the procedures did not introduce a large systematic effect, but they did note that ob-

served fertilization rates may slightly underestimate the true fertilization rate.

In 1994 we assessed overall fertilization rates as well as spatial variation in fertilization. Overall fertilization rates were determined from eggs collected 5 m downstream of all of the *P. porosa* colonies on each night of spawning. The exact position of the diver collecting the eggs was based on the prevailing current. Lasker *et al.* (1996) have previously shown that in the absence of downstream male colonies, fertilization rates do not differ over the range of 1 to 5 m from a spawning female. Farther downstream eggs became too dilute to be collected in a significant number. To determine where eggs are fertilized, eggs were also collected either at a position 0.5–1 m downstream from a female colony (June 1994) or from the center (labeled C in Fig. 1) of the population (July 1994). Positional effects were also studied in September 1994, when eggs were collected both upstream and downstream of a male colony.

In 1995 the sampling program was designed to measure overall fertilization rates and test for the presence of sperm limitation in the field. All measures of *in situ* fertilization were carried out downstream of the whole population. We also monitored the number of female colonies spawning by examining each female colony on the reef every 15 min and recording the start and end of spawning for each colony. Male spawning was not readily observed; to verify that it had occurred, water samples were collected adjacent to arbitrarily selected male colonies and sperm densities were determined by means of a modification (Swain *et al.*, 1997) of the acridine orange direct count technique (Hobbie *et al.*, 1977).

An InterOcean S4 current meter was used to estimate the speed and direction of water flow. The current meter was placed within the population, 1.5 m above the bottom, at the height of most colonies. The S4 meter sampled continuously at 0.5-s intervals starting 15 min before spawning and continuing until egg release had ended.

Sperm limitation was tested in enrichment experiments similar to those described by Lasker *et al.* (1996) for *Plexaura kuna.* One experiment was conducted during each month of spawning in 1995 (3 nights). Eggs were collected on the reef in syringes as described above. Two divers collected side by side, downstream of the whole population. During all three experiments the current ran to the south, and the divers were located at position S (Fig. 1). The eggs, which float, were captured about 3 m above the substratum in the 6-m water column. Collection began at the start of the spawning event and continued for about 60 min, yielding 13 to 15 pairs of samples (55–60 eggs per sample). The samples were then transported to the STRI field station where the paired samples were pooled. From each group of eggs, 50 were incubated with sperm-free water and another 50 with water from an aquarium containing a male colony. As in the field samples, eggs were assayed the following morning to determine the proportion fertilized. As a positive control, 50 virgin eggs were incubated in water from the male aquarium colony. Three replicate controls were set up at the beginning and again at the end of the enrichment process (about 25 min later). The colony explants used to obtain virgin eggs and sperm were collected from Korbiski reef 2–3 days before spawning. Explants were maintained in 18-liter aquaria, and the water was vigorously exchanged every 2 h between 0600 and 1800 h and then once in the evening (2200–2400 h). Water samples from the male tank were collected at the time of the experiment, and sperm density was estimated following the protocol of Swain *et al.* (1997).

Results

Spawning

Spawning in *P. porosa* was highly synchronized in a restricted 2–4 day period that started 5–6 days after the full moon each month from June to September. Scattered observations from the summer months of 1987 through 1995 (36 observation nights) showed that all spawning events occurred 5–10 days after the full moon. Monthly spawning events were characterized by 1–2 nights of intense spawning and 1–2 nights of weak spawning. Usually, the first and the last nights had weak spawning. Most colonies started spawning between 1815 and 1915 h and ended between 1915 and 1945 h. Differences in the timing of egg release between specific colonies were consistent between months and years. Female colonies began spawning by releasing eggs at a low rate for about 10 min. Egg release steadily increased over 15–30 min and then rapidly decreased at the end of the spawning. Sometimes female colonies had two peaks of intense spawning during a single night.

Spatial distribution of colonies

In the study area the density of colonies taller than 50 cm was 0.1 colonies per square meter. The population of colonies with identifiable gonad consisted of six male colonies (height = 125–230 cm, mean = 194 cm), and six female colonies (height = 101–201 cm, mean = 142 cm). Samples collected at either of the two downstream collecting positions (N and S; Fig. 1) had similar mean distances to the six male colonies (N—distance = 4–19.7 m, mean = 13 m; S—6–23 m, mean = 14.8 m). Collections at the central position (C; Fig. 1) always excluded half of the male population as a result of the unidirectional flow regime. The center collection site had a similar mean distance to male colonies (center position

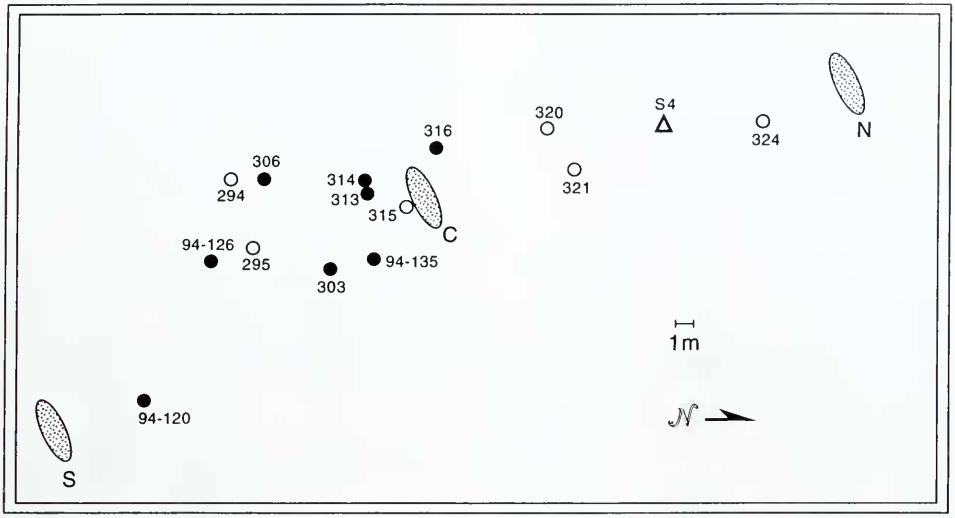

Figure 1. Map of *Pseudoplexaura porosa* colonies (taller than 50 cm) at Korbiski reef, San Blas Is., Panama. Female colonies (filled circles), male colonies (empty circles), and S4 current meter (triangle). Collections were made at positions downstream of the entire population (N or S) and one position in the center of the population (C).

with current from the north—3 colonies at a distance of 3.4–10 m, mean = 5.6 m; center position with current from the south—3 colonies at a distance of 1.8–7 m, mean = 5.1 m).

Variability in fertilization

In situ fertilization ranged between 0% and 98%. The majority (66%) of the downstream samples had levels of fertilization above 50%. The modal fertilization rate was 80%–90% in both years (Fig. 2). Fertilization rates did not differ significantly between years, but did vary significantly between months and days (Tables I and II). The lowest monthly mean was observed in September. Fertilization was high on at least one night during each month (Table II). Annual fertilization success during 1995 was estimated by weighting the fertilization rate of each night by the number of female colonies observed spawning (Table II; Fig. 3), yielding an estimated fertilization rate of 67%. Sperm release was not visible in the field, and measures of sperm density were highly vari-

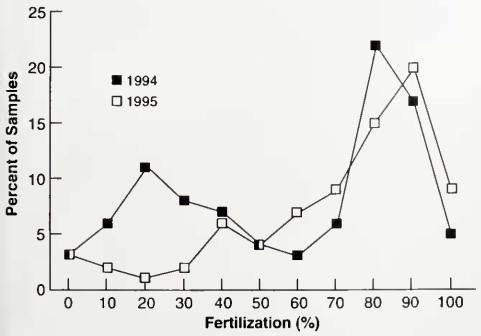

Figure 2. Frequency distribution of fertilization rates among all samples of *Pseudoplexaura porosa* eggs from all nights.

Table I

Nested analysis of variance of fertilization rates of Pseudoplexaura porosa *between years, among months, and among days (months nested in years, and days nested in months)*

Source	df	SS	MS	*F*	*P*
Year	1	0.004	0.004	0.32	0.5717
Month	6	19.87	3.31	281.27	<0.0001
Day	8	14.65	1.83	155.61	<0.0001
Error	152	1.79	0.12		

df, degrees of freedom; SS, sums of squares; MS, mean square; *F*, *F* ratio; *P*, probability.

Table II

In situ *fertilization rate of* Pseudoplexaura porosa *at Korbiski*

Date	No. samples	No. eggs collected	Fertilization rate*			No. ♀ colonies spawning	Sperm density†	Flow	
			Day	Month	Year			cm/s	dir (°N)
1994									
29.VI	16	772	71			—	—	—	
30.VI	19	1023	46			—	—	—	
1.VII	12	367	9	47		—	—	—	
28.VII	16	724	31			—	—	—	
29.VII	21	507	73			—	—	—	
30.VII	31	1757	83	66		—	—	—	
28.VIII	17	615	75			—	—	—	
29.VIII	1	46	57	66	60	—	—	—	
25.IX	9	473	27			—	—	7.0	344
26.IX	12	602	16	22		—		13.3	352
1995									
18.VI	11	530	48			3	—		
19.VI	26	1300	82			5		—	
20.VI	8	481	30	53		1	190	11.2	335
17.VII	3	132	0			1	—		
18.VII	12	709	69			6	1780		
19.VII	26	1300	83	51		6	5200	13.3	148
16.VIII	8	448	40			4	60		
17.VIII	30	1500	85	63	55	5	2370	3.1	51

* Daily, monthly, and annual mean percentages.
† Cumulative sperm/ml.

able, ranging from 0 to 2700 sperm/ml for samples collected from the same male. There was no correlation between fertilization and cumulative sperm release for those nights. Because we could not see sperm coming from the colony, it is unclear whether the variation in sperm density reflects sperm release or the positioning of the sample bottle relative to the "plume" of sperm being released. Assuming that gamete release must be somewhat synchronous between sexes, we also used the number of spawning females as an indicator of the number of spawning male colonies. The number of spawning female colonies explained 80% of the variance in fertilization success observed between nights (Fig. 3).

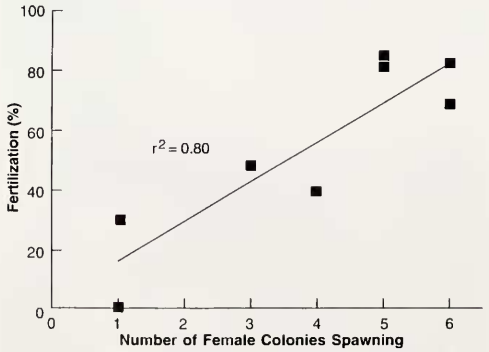

Figure 3. Relationship between number of female colonies spawning and mean daily fertilization rates for *Pseudoplexaura porosa* eggs.

Spatial variability was examined in experiments using three different designs. Fertilization rates among eggs collected close to the colonies versus those collected downstream of the whole population changed significantly, but the effect varied between nights (Table III). There also was a significant day × position interaction.

Table III

Analysis of variance testing for fertilization rates of Pseudoplexaura porosa *collections carried out close to a spawning female colony and downstream of the population (Position), and among days (Day)*

Source	df	SS	MS	*F*	*P*
Day	2	1.11	0.56	26.86	<0.0001
Position	1	0.10	0.10	4.81	0.0348
Day × Position	2	0.31	0.16	7.51	0.0019
Error	36	0.75	0.02		

df, degrees of freedom; SS, sums of squares; MS, mean square; *F*, *F* ratio; *P*, probability.

On two nights, the fertilization rate 1 m from a female colony was lower than the downstream fertilization rate (29 June 1994: 26% at 1 m vs. 71% downstream; 30 June 1994: 3% at 1 m vs. 9% downstream), but on a third night, fertilization close to the female colony was higher than fertilization downstream (63% at 1 m vs. 46% downstream). On 30 June 1994, a third diver also collected samples immediately downstream of the spawning female. The difference between the two collections made at the female colony, 38% and 3%, is indicative of the spatial variability in fertilization rates. Given the variation between divers at the colony, it is not surprising that there were no significant differences between the samples collected at the colony and those collected downstream of the population (ANOVA, $F_{2,9} = 3.02$, $P = 0.099$). However, it is also important to note that relatively few samples were collected that night, which was the last night of spawning.

On 29 and 30 July 1994, a position effect was observed between collections from the center of the population and those downstream. Fertilization was higher at the downstream position than at the position in the center of the population (two-way ANOVA; $F_{1,48} = 33.10$, $P < 0.0001$; Fig. 4). Another experiment (26 Sept 1994) compared the fertilization rates between eggs collected immediately upstream of a male colony and those collected downstream of the male. There was total failure upstream and 16% fertilization downstream (one-way ANOVA, $F_{1,11} = 117.22$, $P < 0.0001$). The low fertilization rate probably occurred because this was the last night of spawning in September and few colonies released gametes. Examination of polyps of colonies sampled 3 days before the September spawning showed that the colony used in the experiment was the only male colony with mature spermaries.

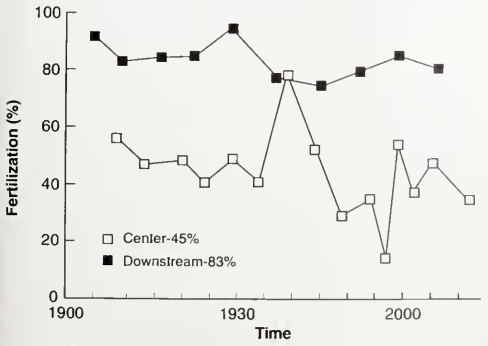

Figure 4. Proportion of *Pseudoplexaura porosa* eggs fertilized in individual samples collected on 29 July 1995 at the center of the population (center) and downstream of the entire population (downstream). Mean fertilization rate at each collection site is also shown.

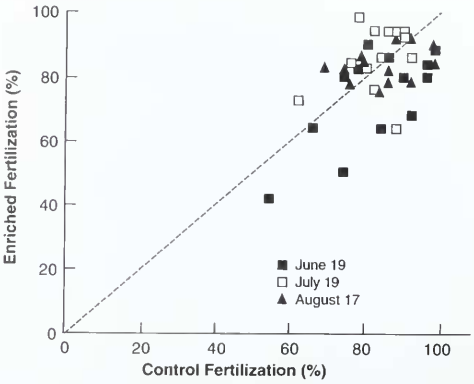

Figure 5. Fertilization rates among in situ samples of *Pseudoplexaura porosa* eggs incubated with (enriched) and without (control) additional sperm.

Sperm-limitation experiments

Enrichment experiments were conducted on a single evening each month during the 1995 spawning events. To ensure an adequate supply of eggs, the enrichment experiments were conducted on the nights with the greatest density of eggs in the water column (19 June, 19 July, and 17 August). Those were the days on which the greatest number of spawning females were observed and *in situ* fertilization rates were over 80% (Table II). There were no significant differences between field fertilization and sperm-enriched samples (paired t test, $t = 1.39$, df = 39, $P = 0.174$; Fig. 5), indicating that sperm limitation did not occur on these three nights. Control incubations carried out in the laboratory at the beginning of the experiment always had fertilization rates higher than 80% (81%–82%) and did not differ from controls initiated at the end of the experiment (two-way ANOVA, $F_{1,8} = 1.25$, $P = 0.296$).

The limited data on flow speed suggests that flow over the range of observed speeds had little impact on fertilization. For instance, fertilization was greater than 80% on both 19 July and 17 August 1995 despite the fourfold difference in current speed on the two nights (Table II).

Discussion

Fertilization success in *P. porosa* was often substantially less than 100%, and *in situ* rates were often lower than those reported for other broadcast-spawning taxa (Petersen, 1991; Oliver and Babcock, 1992; Babcock and Mundy, 1992; Babcock *et al.*, 1992; Sewell and Levitan, 1992; Petersen *et al.*, 1992). As we previously noted (Lasker *et al.*, 1996), this suggests that *P. porosa* fertiliza-

tion rates are sperm limited at times. There also was a general correspondence between sperm release in 1995 and fertilization rates (Table II), but our data also suggest that most eggs are released under conditions in which sperm are not limiting.

First, we determined that 67% of eggs released over the entire spawning event are fertilized. To calculate average fertilization rates, we weighted the fertilization rate from each night by the number of colonies releasing eggs. The number of eggs being released per colony also varies among nights, and it probably peaks on the same nights that the greatest number of colonies spawn. Therefore, our weighted averages probably underestimate fertilization.

Second, we did not detect any evidence of sperm limitation in sperm-enrichment experiments, which were conducted on the nights on which most spawning occurs. That 100% fertilization was never observed in those experiments may be a function of biases introduced by the sampling and incubation techniques (Levitan, 1995; Lasker *et al.*, 1996), but those biases would have affected both the controls and treatments. The failure to see enrichment in samples that yielded only 50% fertilization rates (Fig. 5) suggests that eggs in those particular incubations were less capable of developing, due either to natural variation in gamete quality, or to the experimental technique. In either case the conclusion that sperm were not limiting is not affected.

Spatial variability in fertilization

Lasker *et al.* (1996) showed that eggs collected within 1 m of a colony of *Pseudoplexaura sp.* had similar fertilization rates to eggs collected downstream. Presumably sperm are continuously diluted as they are transported downstream, so eggs released into the water column interact with ever decreasing concentrations of sperm. Therefore, eggs that are not rapidly fertilized will have ever decreasing probabilities of being fertilized. Of course, downstream additions of sperm can affect fertilization. Fertilization rates that we measured did not consistently vary between eggs collected within a meter of the colony and those collected downstream of the entire population, but collections made in the center of the population regularly underestimated the fertilization success of the population. Whether fertilization increased downstream of individual female colonies was probably a function of the behavior of the nearby male colonies, and that effect appears to have varied among nights and colonies. Distance had a positive effect on fertilization when downstream transport enabled eggs to travel past additional male colonies.

Temporal variability in fertilization

Fertilization was very similar in both years. The significant difference between months was mainly due to the low fertilization rate in September. Monthly variation can probably be attributed to gamete release (Ross and Lasker, unpubl. data) or to monthly changes in fertilization kinetics similar to that observed in *Plexaura kuna* (Lasker and Stewart, 1993 and unpubl. data) and in *Acanthaster planci* (Benzie and Dixon, 1994).

Individual size and local population density have significant effects on fertilization rates among echinoderms (Levitan, 1991; Levitan and Young, 1995), presumably through their effects on sperm density in the water column. Sessile organisms cannot aggregate, but synchronization of spawning increases the likelihood of fertilization. The importance of spawning synchronization is evident in *P. porosa* because most of the variance in fertilization among nights was explained by the number of spawning colonies. Although our measure of sperm density did not correlate with fertilization rates, the correlation between fertilization and the number of spawning colonies is likely a reflection of the density of gametes in the water column. This is well illustrated in the 26 September 1994 data which show that when few colonies spawned, most eggs were not fertilized. Conversely, on nights when most of the spawning occurred, fertilization rates were highest and the enrichment experiments revealed no evidence of sperm limitation.

Reproductive strategy and fertilization success

Fertilization rates were low on some nights and sperm limitation probably did occur on those nights; nevertheless, the overall effect of sperm limitation on fertilization success in *Pseudoplexaura porosa* may be low. This result is in marked contrast to the low *in situ* fertilization rates reported for *Briareum asbestinum* (Brazeau and Lasker, 1992) and *Plexaura kuna* (Lasker *et al.*, 1996). Furthermore, the sperm-enrichment experiments failed to detect sperm limitation with *P. porosa*, whereas the results of identical experiments at the same study site strongly suggested sperm limitation with *P. kuna* (Lasker *et al.*, 1996).

Although few octocorals have been examined, we can compare gorgonians for which there are data to assess the effects of life-history traits on fertilization success. At Korbiski and at many sites at which it is common, *P. porosa* dwells at relatively low density in habitats with fast (>10 cm/s) unidirectional currents. Models of fertilization processes predict low fertilization rates under these conditions (Levitan and Young, 1995). However, fertilization rates are higher in *P. porosa* than in other gorgonians, a feature that is probably explained by traits

such as gamete production, fertilization kinetics, spawning pattern, egg size, polyp size, and colony growth rate.

Gamete density—and in particular sperm density—is one of the principal factors determining fertilization success (egg density has only a small effect on fertilization: Lillie, 1915; Vogel *et al.*, 1982; Levitan *et al.*, 1991). *P. porosa*, which is not sperm limited, has spermaries that are an order of magnitude greater in volume than those of *Plexaura kuna*, which is sperm limited (Lasker *et al.*, 1996); and *P. porosa* has the largest spermaries (0.8 mm^3/polyp; Ross and Lasker, unpubl. data) found among the studied gorgonian species (*Briareum asbestinum*, 0.05–0.15 mm^3/polyp, Brazeau and Lasker, 1990; *Paramuricea clavata*, 0.4 mm^3/polyp, Coma *et al.*, 1995b; *Plexaura kuna*, 0.07 mm^3/polyp, Lasker and Stewart, 1993; *Plexaura flexuosa*, 0.05 mm^3/polyp, Beiring and Lasker, unpubl. data).

Spawning synchrony also plays an important role in determining gamete density and fertilization success (Thorson, 1946; Harrison *et al.*, 1984; Sewell and Levitan, 1992). *P. porosa* spawning was limited to about 1 h on each of 4 nights during each of 4 months. Furthermore, most spawning occurred on only 2 of the 4 nights each month. A short spawning period should generate higher gamete concentration than a long spawning period. Spawning over several months allows greater total gamete production, whereas spawning over several days within each month increases the chances of spawning on nights with favorable conditions for fertilization.

Preliminary experiments (unpubl. data) have shown that, in addition to producing many sperm, at least some gorgonians produce gametes that are able to fertilize a large percentage of eggs (>70%) at low sperm concentration (10^2 sperm/ml). This suggests that the fertilization kinetics of *P. porosa* could yield higher levels of fertilization at lower sperm concentration than can be achieved by other broadcast-spawning taxa (sea urchins—Vogel *et al.*, 1982; Levitan *et al.*, 1991; corals—Oliver and Babcock, 1992).

Levitan (1993, 1996a,b) has argued that large eggs present a larger target for sperm and thus increase the probability of fertilization. *P. porosa* eggs are among the largest (700–750 μm, Ross and Lasker, unpubl. data) observed in gorgonians (*Corallium rubrum:* 300–330 μm, Vigni, 1970; *Muricea californica:* 700 μm, *M. fructicosa:* 600 μm, Grigg, 1977; *Plexaura homomalla:* 315–640 μm, Martin, 1982; *Plexaura kuna:* 500–600 μm, Brazeau and Lasker, 1989; *Briareum asbestinum:* 600–900 μm, Brazeau and Lasker, 1990; *Paramuricea clavata:* 400–500 μm, Coma *et al.*, 1995a). *P. porosa* polyps are the largest among gorgonian species in which reproduction has been studied. This trait is important because a large proportion of the fully mature polyp is occupied by gonad, so polyp size may limit gamete production.

Large colony size also contributes to total gamete release, and *P. porosa* colonies are large relative to other reef gorgonians. *P. porosa* also has the fastest growth rate observed among studied gorgonian species (up to 20 cm/year, unpubl. data). Energetic constraints (Harrison and Wallace, 1990) or polyp internal space may limit colony reproductive output. Regardless of the proximal factors controlling growth and reproduction, *P. porosa* colonies inhabit environments that enable them to produce large colonies through fast growth; this, in turn, promotes the production of a large number of gametes at a single point.

P. porosa is common in areas of high flow. Flow affects processes such as feeding, metabolic rate, fertilization, fragmentation, and survival. Although flow may enhance traits such as feeding, and thus the energy balance of a colony, high flow probably reduces the rate of fertilization. The adverse effects of flow rate on fertilization have been observed in many species (Pennington, 1985; Levitan *et al.*, 1992; Petersen *et al.*, 1992; Levitan and Young, 1995; Levitan, 1996a; Coma and Lasker, 1997). However, on the nights we monitored fertilization, the number of spawning colonies appeared to have a greater effect than flow. For instance, on the nights of 19 July and 17 August 1995, a large percentage of the population released eggs and fertilization was over 80%, yet flow on the two nights varied fourfold (Table II). *P. porosa* life-history traits probably reduce the effects of flow on fertilization and thus reduce the importance of sperm limitation.

The Korbiski population produced an estimated 2.1×10^6 eggs (839 branches × 50 cm/branch [minimum estimation of reproductive tissue per branch] × 70 polyps/cm [SD = 14, $n = 10$] × 4.3 eggs/polyp [Ross and Lasker, unpubl. data]). The six mature colonies of the studied population were distributed over an area of 150 m^2; if 67% of all eggs were fertilized, then 56,000 embryos/m^2 were produced annually. This estimate of larval production is similar to that for *Eunicella singularis* (60,000 larvae/m^2; Theodor, 1967). The production of eggs in *P. porosa* (84,000 eggs/m^2) at Korbiski is an order of magnitude smaller than that documented for *Paramuricea clavata* (730,000 eggs/m^2; Coma *et al.*, 1995b). *P. clavata* has a reproductive biology (Coma *et al.*, 1995a) similar to that of *B. asbestinum*, and *B. asbestinum* has fertilization rates that are an order of magnitude lower than those of *P. porosa* (Brazeau and Lasker, 1992).

The life history of *P. porosa* is affected by a wide variety of factors. For instance, polyp size affects feeding as well as gonad volume; egg size may affect larval longevity; growth rates affect maturation and relative probabil-

ities of survival. It is simplistic to argue that the life history of *P. porosa* is built around fertilization success alone, because selection to increase fertilization rate will be balanced by selection on other life-history traits and limited by morphological constraints (Levitan, 1995). Nonetheless, it is clear that many *P. porosa* life-history traits are successful at enhancing fertilization compared with that of species without such traits. Although all eggs were not fertilized and fertilization rates were variable, sperm limitation was not regularly observed. Sperm limitation probably plays a lesser role in the population ecology of *P. porosa* than of other gorgonians.

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